PHILOSOPHICAL TRANSACTIONS.

XI. *On the Causes which influence the Direction of the Growth of Roots.* *By* T. A. Knight, *Esq. F. R. S.* *In a Letter to the Right Hon. Sir* Joseph Banks, *Bart. K. B. P. R. S.*

Read March 7, 1811.

I HAVE shewn, in a former communication, the effects of centrifugal force upon germinating seeds; from which I have inferred that the radicles are made to descend towards the earth, and the germs, or elongated plumules, to take the opposite direction, by the influence of gravitation; and I believe the facts I have stated to be sufficient to support the inferences I have drawn.* But the fibrous roots of plants, being much less succulent, though not uninfluenced in the directions they take by gravitation, are, to a great extent, obedient to other laws, and are generally found to extend themselves most rapidly, and to the greatest length, in whatever direction the soil is most favourable: whence many naturalists have been disposed to believe that these are guided by some degrees of feeling and perception, analogous to those of animal life.

I shall proceed to state some of the facts upon which this

* Phil. Trans. 1806, 1st Part, page 5.

hypothesis has been founded, and others which have occurred in the course of my own experience, and which are favourable to it; after which I shall endeavour to trace the effects observed to the operation of different causes.

When a tree, which requires much moisture, has sprung up, or been planted, in a dry soil, in the vicinity of water, it has been observed, that much the largest portion of its roots has been directed towards the water; and that when a tree of a different species, and which requires a dry soil, has been placed in a similar situation, it has appeared, in the direction given to its roots, to have avoided the water and moist soil.

A tree growing upon a wall, at some distance from the ground, and consequently ill supplied with food and water, has also been observed to adapt its habits to its situation, and to make very singular and well directed efforts to reach the soil beneath, by means of its roots.* During the period in which it is making such efforts, little addition is made to its branches, and almost the whole powers of the plant appear to be directed to the growth of one or more of its principal roots. To these much is in consequence annually added, and they proceed perpendicularly towards the earth, unless made to deviate by some opposing body: and as soon as the roots have attached themselves to the soil, the branches grow with vigour and rapidity, and the plant assumes the ordinary habits of its species.

DU HAMEL caused two trenches to be made so as to intersect each other at right angles, and a tree to be planted at the point of intersection; and taking up this tree some years afterwards, he found that the roots had almost wholly

* SMITH's Introduction to Botany.

confined themselves to the trenches, in which the soil of the former surface must have been buried.

A trench which was twenty feet long, six wide, and about two deep, was prepared in my garden, in the bottom of which trench was placed a layer, about six inches deep, of very rich mould, incorporated with much fresh vegetable matter. This was covered, eighteen inches deep, with light and poor loam, and upon the bed thus formed, seeds of the common carrot *(Daucus carota)* and parsnip *(Pastinaca sativa)* were sowed. The plants grew feebly till near the end of the summer, when they assumed a very luxuriant growth, grew rapidly till late in the autumn, and till their leaves were injured by frost. The roots were then examined, and were found of an extraordinary length, and in form almost perfectly cylindrical, having scarcely emitted any lateral fibrous roots into the poor soil, whilst the rich mould beneath was filled with them.

In another experiment of the same season, the preceding process was reversed, the rich soil being placed upon the surface, and the poor beneath. The plants here grew very luxuriantly, and acquired a considerable size early in the summer; and when the roots were taken up in the autumn, they were found to have assumed very different forms. The greater part had divided into two or more unequal ramifications, very near the surface of the ground, and those which were not thus divided tapered rapidly to a point at the surface of the poor soil, into which few of their fibrous roots had entered.

In other experiments seeds of almost all the common esculent plants of a garden were so placed that the young plants had an opportunity of selecting either rich, or poor soil;

which was disposed, in almost every possible way, within their reach; and I always found abundant fibrous roots in the rich soil, and comparatively few in the poor.

The following experiment afforded the most remarkable result, and one the least favourable to the hypothesis which I have advanced in a former Paper,* and to the conclusion which I shall now endeavour to support; and therefore I think it necessary to describe it very minutely. Some seeds of the common bean (*Vicia faba*), the plant with which many former experiments were made, were placed upon the surface of the mould in garden pots, in rows which were about four inches distant from each other. A grate, formed of slender bars of wood, was then adapted to the surface of each pot, so as to prevent both the mould and the seeds falling out, in whatever position the pots might be placed; and the bars were so disposed, as not at all to interfere with the radicles of the seeds, when protruding. The pots were then directly inverted; and the seeds were consequently placed beneath the mould; but each seed was so far depressed into the mould, as to be about half covered: by which means each radicle, when first emitted, was in contact with the mould above, and the air below. Water was then introduced through the bottom of the inverted pot, in sufficient quantity to keep the mould moderately moist; and, the pots being suspended from the roof of a forcing house, the seeds soon vegetated.

In former experiments,† wherever the seeds were placed to vegetate at rest, the radicles descended perpendicularly downwards, in whatever direction they were first protruded; but under the preceding circumstances they extended hori-

* Phil. Trans. 1806, page 1. † Ibid.

zontally along the surface of the mould, and in contact with it; and in a few days emitted many fibrous roots upwards into it: just as they would have done, if guided by the instinctive faculties and passions of animal life; and as I concluded before I made the experiment that they would do, under the guidance of much more simple laws, whose mode of operating I shall endeavour to explain.

Whatever be the machinery by which the sap of trees is raised to the extremities of their branches, it is obvious that this machinery is first put into action by the stems and branches, and not by the roots: for the graft or bud, whenever it has become fully united to the stock, wholly regulates the season and temperature, in which the sap is to be put in motion, in perfect independence of the habits of the stock; whether those be late or early. If all the branches of a tree, exclusive of one, be much shaded by contiguous trees,* or other objects, the branch which is exposed to the light attracts to itself a large portion of the ascending sap, which it employs in the formation of leaves and vigorous annual shoots, whilst the shaded branches become languid and unhealthy. The motion of the ascending current of sap appears therefore to be regulated by the ability to employ it in the trunk and branches of the tree; and this current passes up through the alburnum, from which substance the buds and leaves spring. But the sap which gives existence to, and feeds the root, descends through the bark;† and if the operation of light give ability to the exposed branch to attract and employ the ascending or alburnous current of sap, it appears not improbable that the operation of proper food and moisture in the soil,

* Phil. Trans. 1805 and 1809, p. 8. † Phil. Trans. 1809, 1st Part, p. 1.

upon the bark of the root, may give ability to that organ to attract and employ the descending, or cortical current of sap; and if this be the case, an easy explanation of all the preceding phenomena immediately presents itself.

A tree growing upon a wall, and unconnected with the earth, will almost of necessity grow slowly, and as it must be scantily supplied with moisture during the summer, it will rarely produce any other leaves than those which the buds contained, which were formed in the preceding year. Some of the roots of a tree, thus circumstanced, will be less well supplied with moisture than others, and these will be first affected by drought: their points will in consequence become rigid and inexpansible, and they will thence generally cease to elongate at an early period of the summer. The descending current of sap will be then employed in promoting the growth and elongation of those roots only, which are more favourably situated, and those, comparatively with other parts of the tree, will grow rapidly. Gravitation will direct these roots perpendicularly downwards, and the tree will appear to have adopted the wisest and best plan of connecting itself with the ground: and it will really have employed the readiest means of doing so, as effectively as it could have done, if it had possessed all the feelings and instinctive passions and powers of animal life. The subsequent vigorous growth of such a tree is the natural consequence of an improved and more extensive pasture.

When the seeds of the carrot and parsnip, in the experiments I have stated, were placed in a poor superficial soil, but which permitted the roots of the plants to pass readily through it, these were conducted downwards by gravitation; whilst

the plants grew feebly, because they received but little nutriment. The roots were in a situation analogous to that of the stems of trees in a crowded forest; and when the leading fibres of the roots came into contact with the rich mould, they acquired a situation correspondent to that of the leading branches of such trees, which are alone exposed to the light. The form of the roots of the plants was consequently long, slender, and cylindrical, like the stems of such trees. The roots of the one required the actual contact of proper soil and nutriment; and the branches of the other required the actual contact of light, to promote their growth.

When, on the contrary, the seeds of the preceding species of plants were placed in a rich superficial soil, their situation was analogous to that of a tree fully exposed, on every side, to the light, whose branches would be extended, in every direction, immediately above the surface of the ground: and as the fibrous roots of the plants came into contact with the subsoil, which was not well calculated to promote their growth, their situation became analogous to that of shaded branches; and they consequently ceased to extend downwards. The fibrous roots of a tree, under similar circumstances, would have extended along the lower surface of the favourable soil; but after these roots had much increased in bulk, they would be found partly compressed into the subsoil, however poor and unfavourable, provided it contained no ingredients actually noxious. In obedience to similar laws, the roots of an aquatic tree will not extend freely in dry soil, nor those of a tree which requires but little moisture in a wet soil; and on this account the roots of the one will appear to have sought, and those of the other to have avoided, the contiguous water;

though both, in the first period of their growth, pointed their roots alike in every direction.

When the seeds of the bean, in the experiment I have described, were placed to vegetate beneath the mould of an inverted pot, a sufficient quantity of moisture was afforded by the mould to occasion the protrusion of the radicles: but as soon as the under points of these had penetrated through the seed-coats, their surfaces were necessarily exposed to dry air, and were consequently rendered rigid and inexpansible; whilst their upper surfaces, being in contact with the moist mould, remained soft and expansible. If both the upper and lower surfaces of the radicles, at their points, had been equally well supplied with moisture, gravitation would have attracted the sap to the lower sides, where new matter would have been added; and the radicles would have extended perpendicularly downwards, as in former experiments: but the influence of gravitation was, to a great extent, counteracted by the effects of drought upon the lower sides of the radicles, nearly as it was counteracted by centrifugal force, when made to act horizontally.*

As soon as the radicles had acquired sufficient age and maturity, efforts were made by them to emit fibrous roots; when want of proper moisture on the lower sides prevented their being protruded, in any other direction, except upwards. In that direction therefore they were alone emitted, (as I was confident that they would before I began the experiment) and having found proper food and moisture in the pots, they extended themselves upwards through more than half the mould, which these contained.

* Phil. Trans. 1806, p. 6.

This experiment was repeated, and water was so constantly and abundantly given, that every part of the radicles was kept equally wet; and they then became perfectly obedient to gravitation, without being at all influenced by the mould above them.

In other experiments pieces of alum and of the sulphates of iron and copper were placed at small distances perpendicularly beneath the radicles of germinating seeds, of different species, to afford an opportunity of observing whether any efforts would be made by them to avoid poisons; but they did not appear to be at all influenced, except by actual contact of the injurious substances. The growth of their fibrous lateral roots was, however, obviously accelerated, when their points approached any considerable quantity of decomposing vegetable or animal matter: and when the growth of the roots was retarded by want of moisture, the contiguity of water, in the adjoining mould, though not apparently in actual contact with them, operated beneficially: but I had reason to suspect that the growth of roots was, under these circumstances, promoted by actual contact with the detached and fugitive particles of the decomposing body, and of the evaporating water.

The growth and forms assumed by the roots of trees, of every species, are to a great extent, dependent upon the quantity of motion, which their stems and branches receive from winds; for the effects of motion upon the growth of the root, and of the trunk and branches, which I have described in a former memoir, are perfectly similar.* Whatever part of a root is moved and bent by winds, or other causes, an increased deposition of alburnous matter upon that part soon

* Phil. Trans. 1803, p. 7.

takes place, and consequently the roots which immediately adjoin the trunk of an insulated tree, in an exposed situation, become strong and rigid; whilst they diminish rapidly in bulk, as they recede from the trunk, and descend into the ground. By this sudden diminution of the bulk of the roots, the passage of the descending sap, through their bark, is obstructed; and it in consequence generates, and passes into many lateral roots; and these, if the tree be still much agitated by winds, assume a similar form, and consequently divide into many others. A kind of net-work composed of thick and strong roots is thus formed, and the tree is secured from the dangers to which its situation would otherwise expose it.

In a sheltered valley, on the contrary, where a tree is surrounded and protected by others, and is rarely agitated by winds, the roots grow long and slender, like the stem and branches, and comparatively much less of the circulating fluid is expended in the deposition of alburnum beneath the ground; and hence it not unfrequently happens, that a tree, in the most sheltered part of a valley, is uprooted; whilst the exposed and insulated tree, upon the adjoining mountain, remains uninjured by the fury of the storm.

In all the preceding arrangement, the wisdom of nature, and the admirable simplicity of the means it employs, are conspicuously displayed; but I am wholly unable to trace the existence of any thing like sensation or intellect in the plants: and I therefore venture to conclude, that their roots are influenced by the immediate operation and contact of surrounding bodies, and not by any degrees of sensation and passion analogous to those of animal life; and I reject the latter hypothesis, not only because it is founded upon assumptions, which cannot be

granted, but because it is insufficient to explain the preceding phenomena, unless seedling plants be admitted to possess more extensive intellectual powers, than are given to the offspring of the most acute animal. A young wild-duck or partridge, when it first sees the insect upon which nature intends it to feed, instinctively pursues and catches it; but nature has given to the young bird an appropriate organization. The plant, on the contrary, if it could feel and perceive the objects of its wants, and will the possession of them, has still to contrive and form the organ by which these are to be approached. The writers who have contended for the existence of sensation in plants, appear to have been sensible of the preceding and other obstacles, and have all betrayed the weakness of their hypothesis, in adducing a few facts only which are favourable to it, and waving wholly the investigation of all others.

In the description of the preceding experiments, I fear that I have been tediously minute; but, as I have selected a few facts only from a great number, which I could have adduced, I was anxious to give as accurate and distinct a view of those I stated, as possible.

I am, dear Sir,
with great respect,
sincerely yours,

THO. AND. KNIGHT.

Downton, Jan. 15, 1811.